How visual stimulus dynamics affect mechanisms of interval timing

Dissertation

zur Erlangung des akademischen Grades

Doctor rerum naturalium (Dr. rer. nat.)

im Fach Psychologie

Eingereicht an der Mathematisch-Naturwissenschaftlichen Fakultät II

der Humboldt-Universität zu Berlin

von

Dipl.Psych, M.Sc., Sophie Herbst

Präsident der Humboldt-Universität zu Berlin
Prof. Dr. Jan-Hendirk Olbertz

Dekan der Mathematisch-Naturwissenschaftlichen Fakultät II
Prof. Dr. Elmar Kulke

Eingereicht am 27.03.2014
Verteidigung am 31.10.2014

Gutachter:
Prof. Dr. Niko A. Busch
Prof. Dr. Elke van der Meer
Prof. Dr. Thorsten Schubert

Contents

Zusammenfassung

Zeitwahrnehmung ist untrennbar mit jeder bewussten Erfahrung verbunden und dennoch sind die dieser Empfindung zugrundeliegenden kognitiven Mechanismen nur unzureichend erklärt. Subjektiv wahrgenommene Zeit stimmt oft nicht mit der objektiv vergangenen Zeit überein, was durch Modelle der Zeitwahrnehmung erklärt werden muss. Zum Beispiel werden dynamische Reize als länger andauernd wahrgenommen als statische Reize. Die Divergenz zwischen subjektiver und objektiver Zeitwahrnehmung ist Gegenstand dieser Arbeit, die in drei empirischen Studien untersucht, wie Zeitwahrnehmung durch den Inhalt eines Zeitintervalls und die durch diesen Inhalt hervorgerufenenen perzeptuellen und kognitiven Prozesse beeinflusst wird. Dabei werden Paradigmen aus der Forschung zur visuellen Wahrnehmung mit Aufgaben aus dem Bereich der Zeitwahrnehmung kombiniert und durch Messungen neuronaler Aktivität mittels Elektroenzephalographie (EEG) ergänzt. Der erste Teil der Arbeitet testet Hypothesen, die von sogenannten sensorischen Modellen der Zeitwahrnehmung abgeleitet wurden. Diese Modelle basieren auf der Annahme, dass die Wahrnehmung von Dauer in den selben neuronalen Netzwerken entsteht, die auch den sensorischen Reiz selbst verarbeiten. Unter dieser Annahme müsste jede Eigenschaft des Reizes, welche neuronale Verarbeitung hervorruft, auch zu einem Effekt auf die wahrgenommene Dauer des Reizes führen, auch wenn diese Eigenschaft nicht bewusst wahrgenommen wird. Die Ergebnisse widersprechen dieser Annahme und zeigen, dass nur Eigenschaften der Reize die auch bewusst wahrgenommen werden einen Einflusss auf subjektive Dauer haben. Zweitens wurde untersucht, ob die objektive Anzahl an Veränderungen die ein Reiz während eines Zeitintervalls durchläuft die wahrgenommene Dauer dieses Reizes bestimmt, oder ob die wahrgenommene Dauer sich von der subjektiv wahrgenommenen Stärke der Veränderung, oder deren neuronaler Verarbeitung ableitet. In Übereinstimmungen mit obigem Befund zeigte sich, dass die subjektiv wahrgenommene Stärke der Veränderung die subjektive Dauer bestimmt.

Zusammengenommen sprechen diese Befunde gegen die Annahmen sensorischer Modelle der Zeitwahrnehmung, aber lassen sich mit den Annahmen von Modellen vereinbaren, die eine zentrale innere Uhr beschreiben. Diese sogenannten Modelle der inneren Uhr müssen jedoch auch erklären können, mittels welcher Mechanismen der Inhalt eines Zeitintervalls dessen subjektive Dauer beeinflusst. Im dritten Teil der Arbeit wird untersucht, ob die Dynamik visueller Reize die Zeitwahrnehmung schon während des "Enkodierens" der Zeit beeinflusst, oder erst später wenn eine Entscheidung über die Dauer des Zeitintervalls getroffen wird. Dazu werden elektrophysiologische Korrelate der Zeitwahrnehmung untersucht. Die Ergebnisse zeigen, dass die neuronalen Korrelate der Zeitwahrnehmung nicht die zeitliche Verzerrung widerspiegeln, die durch dynamische Reize hervorgerufen wird. Dies spricht dafür, dass diese Verzerrung auf einer späteren Prozessstufe eintritt. Insgesamt zeigen die Befunde der drei Studien, das Zeitwahrnehmung sich nicht direkt von der sensorischen Reizverarbeitung ableiten lässt. Der Inhalt eines Zeitintervalls scheint einen geringeren Einfluss auf die wahrgenommene Dauer des Intervalls zu haben als ursprünglich angenommen. Theoretische Implikationen der Befunde werden in Bezug auf die zugrundedliegenden Modelle diskutiert und Implikationen für weitere Forschung im Bereich der Zeitwahrnehmung abgeleitet.

Summary

Time perception is a basic subjective experience, but the underlying cognitive mechanisms are not well understood. Often, perceived time differs from objective time. The following work addresses this discrepancy by investigating how perceived time is influenced by the content of a time interval and the perceptual and cognitive processing of this content. It has been shown that dynamic stimuli are perceived as longer than static stimuli. Three empirical studies are conducted to assess how visual stimulus dynamics affect perceived duration. We combine paradigms from vision research with timing tasks and measures of neural processing using electroencephalogram (EEG). The first part of this work tests hypotheses derived from sensory models of interval timing, which claim that duration of a time interval is encoded in the same neural networks that process its sensory content. According to these models, the "neural energy" expended in the sensory processing of a stimulus also codes for the perceived duration of that stimulus. If this is true, even stimulus dynamics that are processed on an automatic sensory level but are not consciously perceived should affect perceived duration. In contrary, we show that only consciously perceived stimulus dynamics affect perceived duration, with more perceived dynamic leading to longer perceived duration. Second, we tested whether the objective number of changes in sensory input relates to perceived duration, or whether the subjective saliency of these changes, or their neural processing explains the effect on perceived duration. In line with the first result, only consciously perceived changes affected perceived duration, but not changes that were not perceived but evoked a neural response (measured in the electroencephalogram, EEG). These findings argue against the assumption of sensory timing models, but are consistent with models that assume a specialized internal clock. However, internal clock models do not sufficiently explain why stimulus dynamics dilate perceived duration. In the third study, we tested whether stimulus dynamics affect the stage of temporal encoding as postulated by internal clock models, or affect duration perception at later processing stages. Since the duration judgment given by the participant does not allow distinguishing between an effect on the encoding and the decision stage, we measured neural correlates of temporal encoding in the EEG. We found that the neural correlates of temporal encoding reflected internal variations in perceived duration, but not the dilation induced by stimulus dynamics. We therefore argue that visual stimulus dynamics affect perceived duration after temporal encoding during the decision process. In sum, our findings show that duration perception is not grounded in early sensory processing, but is probably achieved by a specialized timing system that can be biased by the perception of dynamic stimuli. We discuss the theoretical implication of these findings for theories of time perception, and their implications for further research in this field.

List of original research articles

Study I:

Herbst, S. K., van der Meer, E., Busch, N. A., et al. (2012). Attentional selection dilates perceived duration. *Perception*, 41(8):883.
doi:10.1068/p7300

Study II:

Herbst, S. K., Javadi, A. H., van der Meer, E., and Busch, N. A. (2013). How long depends on how fast — perceived flicker dilates subjective duration. *PloS one*, 8(10):e76074.
doi:10.1371/journal.pone.0076074

Study III:

Herbst, S. K., Chaumon, M., Penney, T. B., and Busch, N. A. (2014). Flicker-induced time dilation does not modulate EEG correlates of temporal encoding. *Brain Topography*, August 2014.
doi: 10.1007/s10548-014-0389-z

List of abbreviations

CNV	contingent negative variation
EEG	electroencephalography
ERP	event related potential
PSE	point of subjective equality
PSE	point of subjective equality
RSVP	rapid serial visual presentation
SSVEP	steady state visual evoked potential

List of figures

The question is important, for, if the experience be what it roughly seems, we have a sort of special sense for pure time? A sense to which empty duration is an adequate stimulus; while if it be an illusion, it must be that our perception of time's flight, in the experiences quoted, is due to the filling of the time, and to our memory of a content which it had a moment previous, and which we feel to agree or disagree with its content now.

WILLIAM JAMES

(James, 1891, p.619)

1 Introduction

1.1 The puzzle of subjective time

Time perception is inseparably linked to subjective experience. Every impression has a duration that we perceive — without any additional effort — together with the impression itself. Unlike other senses, such as light or sound, no dedicated sensory organ exists to subserve time perception. There does not even seem to be a physical substrate of time comparable to light or sound waves that can be extracted from the environment. Nevertheless, timing is so ubiquitous and effortless that we often become aware of it only when we sense a mismatch between subjective and objective time, for example when *a watched pot never boils*, or as *time flies when we are having fun*. The mismatch between objective time and subjective time offers an excellent test case for theories and models of time perception, which to this day remain challenged by the inherently subjective nature of time perception (Kelly, 2005).

As expressed by the sayings above, subjective time is greatly influenced by non-temporal events, for example by the events we perceive during a time interval. The work described here investigates how the content of a time interval affects the perceived duration of this interval.

Researchers have spelled out a number of distinctions that allow to classify the different processes subsumed under the term time perception. This broad term encompasses temporal order judgments, simultaneity judgments, rhythm perception, and the perception of duration (Pöppel, 1978). Duration perception is the concept most closely related to what the lay person refers to when talking about time perception: the subjective extent of an interval in time. Duration perception has been studied on different time scales from milliseconds to years, which involve different cognitive and neural mechanisms (Buhusi and Meck, 2005). This work addresses the time range lasting from hundreds of milliseconds to seconds. The processes underlying perception of durations in this range are often referred to as cognitive timing, or interval timing (Hinton and Meck, 1997). These durations can be accessed consciously (which is difficult for shorter durations), and can be easily studied experimentally, since they are short enough to be presented repeat-

edly (which is difficult for longer durations). Therefore, perception of durations in the so called peri-second range has triggered a host of empirical studies. Different models of how a cognitive system and a biologically realistic brain could account for our perception of these durations have been described.

1.2 Models of interval timing

Models of interval timing can broadly be divided into two categories: models that assume specialized timing mechanisms and models that do not assume specialized mechanisms. Recently, these two different classes of models have been labelled as "dedicated and intrinsic models" (Ivry and Schlerf, 2008).

1.2.1 Dedicated models: the internal clock

Dedicated models constitute the more traditional class of models, which were devised in the light of the information-processing approach. They postulate a modular structure built around a central timer that has been termed an *internal clock*. This timer is not described as a sensory organ which is able to extract time from the environment, but as an intrinsic organ which generates the organism's own time. This timer functions independently of the signal modality (e.g. visual or auditory signals) or the output (e.g. motor response or verbal judgment).

The first descriptions of models with a central timer can be found in Creelman (1962) and Treisman (1963). Upon these initial descriptions different varieties have been built (Gibbon, 1977; Church, 1984; Wearden, 2003). The classical internal clock model (see Figure 1) comprises three stages: a stage of temporal encoding, a stage of memory processing, and a stage of temporal decision making. During temporal encoding, a pacemaker emits regular pulses which are transferred to an accumulator. Many models also postulate a switch between the pacemaker and the accumulator, which governs the amount of pulses that actually reach the accumulator. After temporal encoding, the pulses are transferred from the accumulator to a working memory store and are compared to a previously memorized reference duration. Based on this comparison, a temporal judgment is generated. Internal clock models offer an intuitively plausible description of the cognitive mechanisms of interval timing and have been described in mathematical ways (see e.g. Gibbon, 1977).

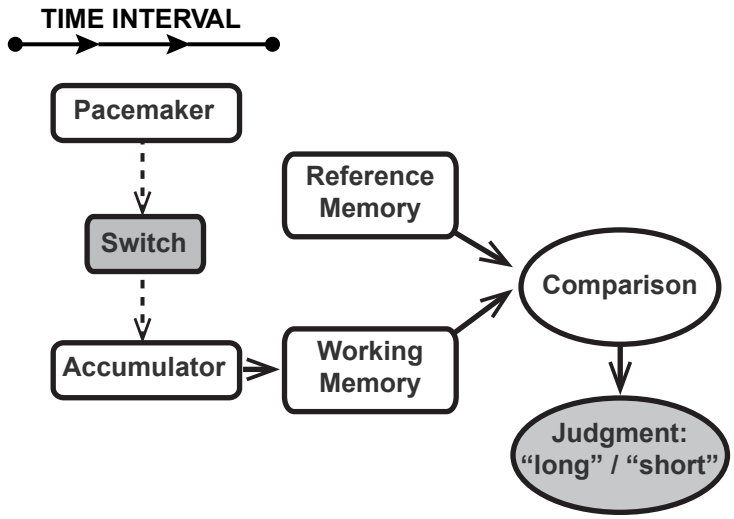

Figure 1: **A model of the internal clock** (adapted from Church (1984) and Wearden (2004)) Internal clock models postulate three stages of temporal processing. During the stage of temporal encoding, a pacemaker emits regular pulses that are transferred to an accumulator unit (displayed as arrows with dotted lines). Several models also postulate a switch between the pacemaker and the accumulator, regulating the flow of pulses between the two modules. At the memory stage following temporal encoding, the pulses are transferred from the accumulator to a working memory store. Finally, at the comparison stage, the stored pulses are compared to a reference duration retrieved from working memory to obtain a judgment about the elapsed duration.

The failure to localize an internal clock in the brain presents a challenge to internal clock models. Several candidate structures have been named, such as the cerebellum (Ivry et al., 2002), basal ganglia (Harrington et al., 1998), supplementary motor area (Macar et al., 1999), or prefrontal cortex (Lewis and Miall, 2006). Timing seems to recruit many different brain structures and seems to be achieved by a network rather than by a dedicated region (Coull et al., 2004).

While the clock as such could not be identified, internal clock models have nevertheless brought forward research on brain processes that reflect specific modules of the clock. Of particular importance to the work presented here is the activity observed in electroencephalographic recordings (EEG) over primary motor areas. A slow negative deflection over these areas, known as the contingent negative variation (CNV, Walter et al., 1964), can be observed when participants are expecting an imperative stimulus or are timing an interval. Several studies have validated the relationship between the CNV component and perceived duration and it has been proposed that the CNV amplitude reflects the process

of temporal accumulation (Macar et al., 1999; Ng et al., 2011; McAdam, 1966). The CNV has therefore been termed *"an on-line index of timing"* (Macar and Vidal, 2004), and can be used to study the ongoing process of temporal encoding during a temporal interval.

A great advantage of internal clock models — and maybe the main reason behind their popularity — is their flexibility in explaining and modelling a wide range of findings observed in different timing tasks. However, the models have also been criticized for being too flexible in accommodating new findings by including a number of components that can interact in various ways (e.g. Staddon and Higa, 1999). For instance, a mismatch between subjective and objective time can be explained by an accelerated clock rate, by a switch which regulates the flow of pulses from the pacemaker to the accumulator, or by effects on the comparison process. Part of the work described here addresses the stage of temporal processing where the mismatch between objective and subjective duration occurs.

1.2.2 Intrinsic models

Intrinsic models do not postulate a mechanism that is specifically dedicated to timing, but rather describe timing as an inherent property of neurons or neuronal networks distributed across the brain. The mechanisms circumscribed under the term intrinsic models are very diverse and range from mathematical descriptions of ramping activity of single neurons (Reutimann et al., 2004) to complex interactions across neuronal networks (Mauk and Buonomano, 2004; Laje et al., 2011). The problem with intrinsic models of interval timing is that while they are very specific with respect to computational mechanisms that allow neuronal units to encode time, they do not clearly specify how a coherent representation of duration is achieved based on these distributed units.

A subclass of intrinsic timing models maintains that duration is encoded by the neuronal populations that are activated by the content of the time interval. In an influential article, Eagleman and Pariyadath (2009) proposed a "neural energy account", which implies that perceived duration is a function of the neural energy exerted to encode the stimulus. Evidence for their proposal comes from the combined interpretation of studies showing that repeated stimuli are judged shorter than novel stimuli (Pariyadath and Eagleman, 2007) and that repeated stimuli evoke a decreased neural response (Grill-Spector et al., 2006). The neural energy approach can explain a number of findings, for example, that rare stimuli are perceived as longer than frequent ones (Tse et al., 2004) or that inter-

vals filled with light or sound appear longer than empty intervals (Rammsayer and Lima, 1991), assuming that the encoding of such stimuli requires different amounts of neural energy. In order to test this account, one needs an exact definition of "neural energy". Eagleman and Pariyadath (2009) remain vague on this point, suggesting that the crucial energy might, for example, reside in brain areas that encode the sensory content of the time interval (p.1844).

The proposal that duration is encoded in sensory areas is supported by a number of findings (for a review see Bueti, 2011). Several studies have shown that low-level attributes of visual stimuli influence subjective duration, for example stimulus intensity (Matthews, 2011), size (Xuan et al., 2007), or frequency (Kanai et al., 2006). Observing that these dynamics trigger specific responses already in sensory areas has lead to the suggestion that temporal processing emerges from the activity during sensory stimulus processing. Some studies explicitly show that perceived duration of visual stimuli reflects properties of neurons in the visual system, such as the local adaptation to flicker (Johnston et al., 2006). Furthermore, timing of visual events can be impaired independently from timing of auditory events (Bueti et al., 2008), suggesting modality-specific encoding of time.

In sum, dedicated and intrinsic models assess duration perception from two completely different angles. Dedicated models postulate a specialized system underlying duration perception. In principle, this system could function without any external input and therefore constitute "a sort of special sense of pure time" (James, 1891). Conversely, intrinsic models, such as sensory models of interval timing, postulate no such specialized system. Here, perceived duration emerges from ongoing perceptual processes, like the encoding of sensory content present during a time interval.

1.3 A sense of time or a sense of change?

A sense of time

Our perception of time is tightly coupled to the content of the respective time interval. For instance, Guyau (1890) describes how the perception of time depends on the number and the intensity of stimuli presented during the interval, and the attention dedicated to them (see also Michon et al., 1988; Roeckelein, 2000).

Can we perceive the duration of an empty interval without any events? Or in the words of James (1891), do "we have a sort of special sense for pure time ?" (see quote on

p.8 of this document). As described above, an intuitively plausible perspective on interval timing is one that assumes mechanisms that function independently of perceptual (and other cognitive) processing (Allan and Kristofferson, 1974). An independent mechanism of interval timing is supported by the experience that we can assess the duration of an empty interval, or compare the durations of two such intervals. Furthermore, durations can be compared across different modalities. Empirical evidence for an independent timing mechanism is provided by studies showing that perceiving and producing a duration relies on a common system (Ivry and Hazeltine, 1995), and that timing of visual and auditory signals follows the same rules (Grondin, 1993). Above, dedicated models of interval timing that postulate specified timing mechanisms have been described, like an internal clock that functions independently of other cognitive processes. These models claim that the timer works based on an internal rhythm (whose nature is still a matter of debate), and that duration can be perceived independently of the content of a time interval.

Research based on this perspective has dedicated less effort to disentangling the influences of sensory interval content on perceived duration, and has rather focused on the mechanisms underlying duration perception. Effects of sensory interval content on perceived duration are treated as distortions or illusions (Eagleman, 2008). Nevertheless, approaches that assume a specific timing mechanism also have to explain how perceived duration is influenced by external factors, like the sensory content of a time interval.

Effects of non-temporal factors present during a time interval on perceived duration (e.g. Xuan et al., 2007; Brown, 1995; Kanai et al., 2006) pose a challenge for internal clock models and can be accommodated only by making additional assumptions. One assumption is that non-temporal magnitude can affect the clock's speed by enhancing the arousal of the organism (Penton-Voak et al., 1996). A different explanation of the effect of non-temporal factors on perceived duration has been brought forward by adding an attentional switch to the model (Block and Zakay, 1996, 1997; Tse et al., 2004). This switch controls the transmission of pulses from the pacemaker to the accumulator, and is itself controlled by the attention allocated to the information that is relevant for the timing task. Therefore, the more attention is allocated to the stimulus the more pulses from the pacemaker reach the accumulator, and the longer the duration appears. Finally, the processing of the sensory content could affect perceived duration at the later stages in the model, after temporal encoding. It has been suggested that the transfer of the accumulated pulses to reference memory can induce variation that in turn biases the

temporal decision of the observer (Church, 1984). In sum, a pure sense of time might exist, generated by an internal clock which is, however, sensitive to influence of non-temporal factors.

A sense of change

James denies the existence of a pure sense of time, saying that "we can no more intuit a duration than we can intuit an extension, devoid of all sensory content" (James, 1891, p.620). Even in the absence of external stimulation, we are always aware of "some changing process", be it even internal rhythms such as heart-beat or breath. Thus, he infers that our perception of time is based on the awareness of change. To illustrate the nature of change, James cites the work of Münsterberg (1889), who states that duration perception relies *"upon the feelings of muscular tension and relaxation"* [...] that are *"primarily in the muscles by which we adapt our sense-organs in attending to the signals used"* (Münsterberg, 1889, p.29). James specifies that these muscles can be in the eyes or ears. The term muscles might be misleading, but the idea that sensory processing provides the basis for perceived duration precedes the sensory models of interval timing described above, and provides an important basis for this work.

The idea that the perception of changes during a time interval provides the basis for perceived duration has greatly influenced the research on duration perception. Fraisse (1963) even suggested that perceived duration is a function of the number of changes perceived during a time interval (p.233). To test this assumption, one needs a very clear definition of the change relevant for duration perception. It is of course not the change itself that leads to the perception of duration, but the perceptual processes in the brain of the observer that extract change from the environment, and transform it into quantifiable units that translate into a percept of duration.

The proposal that the perception of change leads to the perception of duration immediately evokes the question of what is meant by "perception of change". Does the term perception merely imply *processing of change* by some cognitive system, or does it imply *conscious perception of the change* by an observer? This work attempts to separate the processing of change that does not require (or does not lead to) conscious perception from the conscious perception of change. If automatic sensory processing of changes was sufficient for an effect on perceived duration, this would strongly support models that assume a relationship between sensory processing and perceived duration.

On the contrary, if conscious perception of change was a necessary condition for it to affect perceived duration, this would argue for models that postulate a mechanism of timing that is not directly based on automatic sensory processing, and probably functions completely independently of sensory processing.

Change can imply any dynamic aspect of the content of a time interval, including changes in intensity and number, or displacement across space. Many studies have shown that dynamic perceptual properties of the stimuli, such as their frequency (Kanai et al., 2006), size (Xuan et al., 2007), or speed (Kaneko and Murakami, 2009) influence the perceived duration of these stimuli. The problem is that we lack a clear definition of the dynamics relevant for duration perception and an idea of how these dynamics can be quantified. It has never been explicitly asked which of the various events related to the processing of stimulus dynamics are relevant for their effect on subjective duration. Therefore, it is a central endeavour of this work to test whether there is a quantifiable relationship between the number of changes present in the stimulus, and the perceived duration of this stimulus. We will address this question with respect to current models of interval timing which provide different explanations for the effect of stimulus dynamics on perceived duration.

The question whether perceived duration is inherently bound to the perception of the sensory content of a time interval can also shed light on the question whether we have a dedicated sense for time or whether subjective time reflects a percept emerging from other cognitive processes, such as perceived change.

1.4 Visual perception of change

Although basically any sense could be used to test the relationship between the perception of change and the perception of duration, this work is restricted to the visual domain. Visual perception is relatively well understood. We have a general idea about how the processing of basic visual stimuli is achieved by a cognitive system. We also know which brain areas are involved in mediating the transfer of physical energy from the environment to our perception of for example a light. Furthermore, specific neural correlates of the processing of visual stimuli have been described and can be used as a measure of how the visual system processes the sensory content of a time interval. These measures can be tested for their relation to perceived duration, as suggested by sensory models of interval timing and will allow us to test specific hypotheses about the relationship between visual

perceptual processing and duration perception.

The research on visual perception has developed paradigms that make it possible to separate different stages of visual processing. Such paradigms are of interest to this work, since they allow to establish which of the processes related to perceived changes affect perceived duration. Of particular interest to this work are paradigms that allow to separate automatic sensory processing from conscious perception. Such paradigms serve as tools to deliberately assess the influences that each of these processes exerts on duration perception and test whether conscious perception of change is a necessary condition for an effect on perceived duration. Examples of such paradigms are the repetition blindness paradigm (Kanwisher, 1987) and the attentional blink paradigm (Raymond et al., 1992), as well as the flicker fusion paradigm (Landis, 1954). A detailed description of these paradigms and reasons why they are a useful tool for the study of time perception will be given below.

2 Research questions and hypotheses

This work was designed to explore how the visual content of a time interval and its perceptual processing affect perceived duration of the time interval. There is no sensory organ to perceive time. Therefore, it has been suggested that duration perception is based on the perception of changes occurring throughout the time interval. Furthermore, it has even been suggested that duration perception is a function of the *number* of changes perceived during the time interval.

Defining the relationship between perceptual processing of sensory content and duration perception can also shed light on the underlying cognitive mechanisms of duration perception A question that is currently dividing research on interval timing is whether timing is achieved by a specific clock-like mechanism, or whether timing can be achieved in the absence of such a clock. Clock-like models of interval timing assume a specialized timing mechanism that can be biased by the sensory content, but is not directly related to sensory processing. Sensory models of interval timing, on the other hand, postulate that time emerges from the neural processing of sensory content itself and is therefore inherently linked to it. To investigate how the sensory content of a time interval and the cognitive processing of this content affect the mechanisms of duration perception, we addressed the following questions.

- Does the effect of stimulus dynamics on perceived duration depend on conscious perception of these dynamics or does it occur even without conscious perception of the dynamics?

- Does the objective number of changes throughout a time interval explain the perceived duration of that time interval?

- Is the magnitude of the neural processing of the changes an indicator for perceived duration?

- Do perceived changes affect temporal processing during the encoding of the time interval or at a later stage?

Hypothesis I: Perceived duration is a function of the number of changes perceived throughout the time interval.

If this hypothesis is true, perceiving more changes should lead to a monotonic increase of perceived duration.

Hypothesis II: The neural processes responsible for the perceptual encoding of the sensory content of a time interval are the basis for duration perception.

If this hypothesis holds, perceived duration should be influenced even by stimulus dynamics that are only processed on an initial sensory level, but not consciously perceived. In contrary, if perceived duration is influenced only by stimulus dynamics that are consciously perceived, this argues for an interaction between perceptual processing and duration perception at higher cognitive levels. Furthermore, if Hypothesis II is true, a testable relationship between the neural correlates of visual perceptual processing of the stimulus and its perceived duration should exist.

The studies devised to test Hypotheses I–II did not confirm a close relationship between sensory processing and perceived duration. Rather, the results pointed towards mechanisms of interval timing that function independently of sensory perception. Nevertheless stimulus dynamics strongly influenced perceived duration. We therefore devised a third study, to test how perceived stimulus dynamics interact with the temporal mechanisms postulated by the internal clock model. We were specifically interested in the question whether stimulus dynamics affect perceived duration already during the stage of temporal encoding or at a later stage. Therefore, we assessed neural correlates of temporal encoding and tested whether these showed a modulation by the temporal dilation induced by stimulus dynamics.

Hypothesis III: If perceived stimulus dynamics affect the process of temporal encoding during the presentation of the stimulus, they should, besides affecting behavioural duration judgments, also modulate the neural correlates of temporal encoding.

3 General methodological approach

This work consists of three independent studies based on a common approach: to combine paradigms from vision research with timing tasks. Although the tasks differ across the three studies, all studies use psychophysical methods to assess behavioural duration judgments. Studies II and III additionally use EEG recordings. This section will give a brief overview of the common methods applied in the three studies. The individual methods used in each study will be described in the respective summary sections.

3.1 Timing tasks

There are a number of tasks that are classically used to study duration perception in the peri-second range (for a concise review, see Grondin, 2010). Most common tasks are comparison and duration bisection tasks. In the comparison task, participants are presented with two stimuli on each trial and are asked to compare their duration, usually by answering "shorter" or "longer". Sometimes, an "equal" option is also included. One of the stimuli is a standard of constant duration and the other is a test stimulus of constant or varying duration. The task can be made more or less difficult by varying the difference in duration between the test stimulus and the standard. When using equal durations for the standard and test stimuli, one can study internal variation of perceived duration or the effect of an experimental manipulation, as done in Studies I and II.

In the duration bisection task, participants are first familiarized with two reference durations: a short and a long duration. During the actual task, they are presented with only one test stimulus of varying duration on each trial and are asked to judge whether the stimulus is closer to the short or the long reference duration. By varying the difference in duration between the reference durations, and/or the spacing of the intermediate test durations, one can vary the difficulty of the task. Both, the comparison task and the bisection task can be modelled with psychometric functions, if varying test durations have been used.

3.2 Psychophysical modelling

The data produced by the comparison task and the bisection task are typically analysed using psychophysical techniques (as done in Studies I and III). These techniques can even be used during stimulus presentation to select appropriate test stimuli (done in Study

II). Psychometric functions are fitted to the data to model the probability of responding "long" as a function of stimulus duration. The psychometric function has four parameters: a threshold, also termed the point of subjective equality (PSE), a slope, a lower asymptote (guess rate) and an upper asymptote (lapse rate) (for a detailed description, see Prins et al., 2009; Wichmann and Hill, 2001a,b). Of particular importance in timing tasks is the PSE, which describes the stimulus duration at which the observer is maximally unsure about whether the duration was long or short (the 50% threshold), and is therefore as likely to choose either alternative. The PSE is frequently assessed as a measure of perceived duration (Grondin, 2008). The slope of the psychometric function also provides important information about the underlying timing behaviour. Steeper slopes (also referred to as difference limen in the timing literature) are thought to reflect more accurate timing.

3.3 Electroencephalography (EEG)

Duration judgments measured by the timing tasks described above assess the decision of the observer about the duration of a temporal interval that has already elapsed. However, different processes might contribute to this decision, making the duration judgment a very coarse measure of the processes underlying perceived duration. By recording the activity of the brain during the temporal interval, one can gain additional information about the processes that precede the duration judgment. Especially the electroencephalogram (EEG) provides a temporal resolution that is suitable to study the processes during a short time interval in detail. Studies II and III therefore use EEG recordings in addition to the assessment of behavioural duration judgments. EEG is used here to access the brain activity evoked by the stimulus, as a measure of visual (Study II) and temporal (Study III) processing of the stimulus. In Study II, evoked oscillatory responses (the SSVEP) to the flickering stimuli were measured to assess the magnitude of the neuronal response to the flickering stimuli. In Study III, stimulus evoked potentials were measured to assess the neural correlates of temporal processing of these stimuli.

4 Summaries of the three experimental studies

4.1 Study I: Attentional selection dilates perceived duration

4.1.1 Background

Study I examines whether an effect of stimulus dynamics on perceived duration is contingent on the conscious perception of these dynamics, by deliberately separating automatic sensory processing from conscious perception. As described in the Introduction, the research of visual perception has brought forward paradigms that allow to separate the initial sensory processing of a visual stimulus from attention-based processing at higher levels that is necessary for conscious perception of the stimulus. Two very similar paradigms are used in this study: repetition blindness (Kanwisher, 1987) and attentional blink (Raymond et al., 1992). In a rapidly presented stream of visual items (e.g. numbers or letters; for an illustration see Figure 2 left panel) the observer is required to detect specific target items. In repetition blindness experiments all targets presented are identical (e.g. the letter X), while in attentional blink experiments the targets are different but belong to the same category (e.g. numbers presented in a stream of letters). Both paradigms produce a robust effect: a second target presented shortly (but not immediately) after the first is frequently missed. The reduced detection rate for the second target has been explained by a two-stage recognition process: stimuli are first processed on an automatic sensory level to identify potential target candidates. All stimuli pass this initial step. In a second step attention is allocated to the stimuli, individuating them as a unique event in time (Chun, 1997; Treisman and Gelade, 1980). Whenever the second process is still allocated to the preceding target, a subsequent target does not pass the second step, and fails to be detected. It has been shown that even undetected targets pass the first stage of automatic sensory processing, and can for instance facilitate the recognition of subsequent targets due to priming (Shapiro et al., 1997) or evoke an EEG response reflecting semantic processing. Therefore, both paradigms make it possible to assess on the basis of the participants' behaviour whether a target was processed solely on an automatic sensory level or perceived consciously.

Here, we embedded these two paradigms in a duration comparison task. We measured whether perceived duration of the whole stream of items was affected by the number of targets detected in the stream. If target stimuli that are processed only at an automatic

sensory level affect subjective duration as much as fully processed stimuli, this would indicate that automatic sensory processing of stimulus dynamics is sufficient for an effect on perceived duration. If, however, only stimuli that are consciously perceived affect subjective duration, this would show an interaction of the processing of visual stimulus dynamics and the mechanisms of temporal processing at higher cognitive levels.

The study is based on three independent experiments, conducted to (1) test for an effect of target detection on subjective duration, (2) specify the conditions under which this effect occurs, and (3) confirm that the effect is not confounded by the numerical response given in the target counting task.

4.1.2 Methods

Rapid serial visual presentation (RSVP) was used to induce the repetition blindness (Experiments I and II) and attentional blink effects (Experiment III). Duration judgments based on the RSVP streams were acquired on each trial in a comparison task. The standard sequence without any targets was presented prior to the test sequence containing the targets. Participants had to compare the duration of the two sequences in a two-alternatives-forced-choice task (see Figure 2, left panel).

In Experiment I, the RSVP streams consisted of letters and the letter X was assigned as the target. Streams contained either one or two targets. Streams lasted 1.6 s (including 16 items lasting 0.1 s each) and standard and test streams were of equal duration. Catch-trials were intermixed with the experimental trials, in which the duration of the standard sequence was varied. On each trial, participants reported the number of targets seen and indicated whether the test sequence lasted longer or shorter than the standard.

The statistical analysis assessed whether the number of targets presented or the number of targets reported influenced the perceived duration of the sequences. To this end, trials were assigned one of three post-experimental categories: one target presented / one reported, two targets presented / one reported, and two targets presented /two reported. Duration judgments were compared across these three categories.

Experiment II used the same paradigm as Experiment I, but this time we varied the duration of the experimental sequence. The variation of the sequence duration made it possible to fit psychometric curves to the data and model the proportion of trials that were judged as longer at each sequence duration. Again, the trials were split into three post-experimental conditions based on the number of targets presented and reported. We

assessed the threshold and slope parameters of the psychometric curves fitted to the data from each of the three conditions to test at which sequence duration the temporal dilation effect was maximal.

Experiment III used the attentional blink paradigm, in which participants had to detect numbers intermixed with the letter RSVP stream. Instead of counting the targets participants had to report the identity of one or two targets. Again the sequence duration was varied and psychometric curves were fitted to the data to model the relationship between objective and subjective sequence duration.

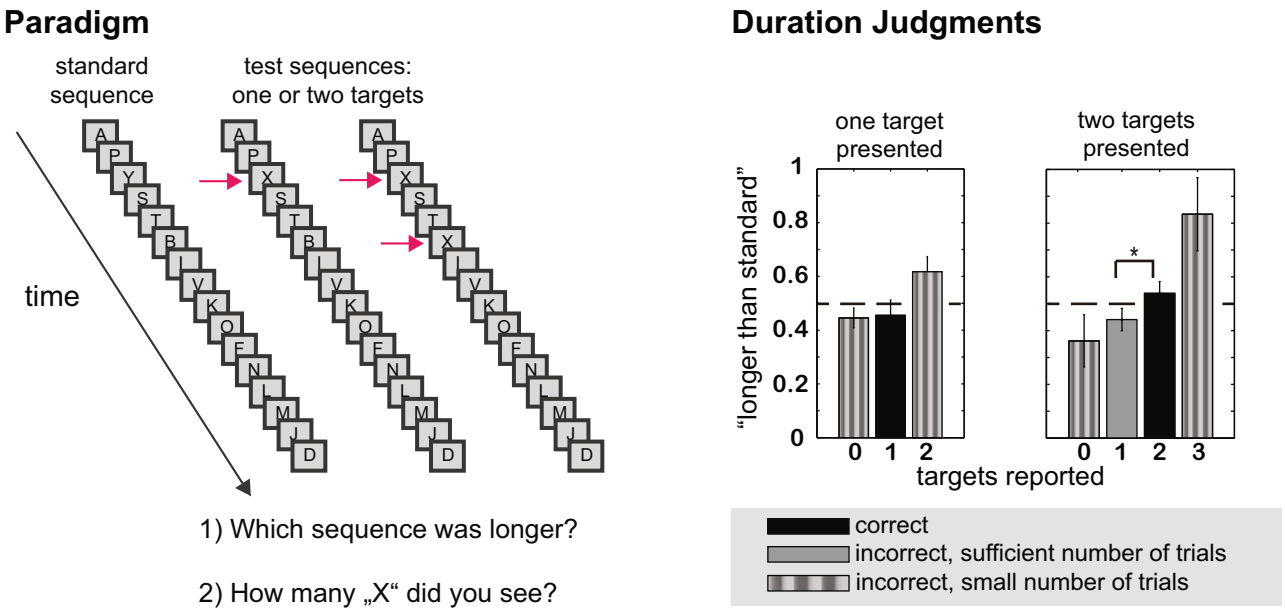

Figure 2: **Study I: Paradigm and Results** (adapted from Herbst et al. (2012), with permission from Pion Ltd, London, *www.pion.co.uk*). **Left panel: RSVP paradigm.** On each trial we presented a standard sequence containing no targets and a test sequence containing one or two targets (the letter X). After the end of both sequences, participants had to answer whether the test sequence lasted shorter or longer than the standard, and whether they detected one or two targets. **Right panel: Results.** The number of targets detected (indicated on the x-axes) affected the proportion of responding "long" (indicated on the y-axes). The left and right insets show sequences in which one target was presented and sequences in which two targets were presented. More targets detected dilated perceived duration. The solid bars indicate conditions in which the number of trials was sufficient to perform statistical tests (* indicates $p < 0.05$). The striped bars indicate conditions for which the number of trials was too low (e.g. two targets presented / zero reported) to perform statistical tests. The number of targets presented did not affect perceived duration.

4.1.3 Results

Experiment I showed the classical repetition blindness effect: a second target in an RSVP stream was detected less often than a single target and its detection depended on the temporal spacing of the two targets. Importantly, the number of detected targets affected the subjective duration of the whole RSVP stream: streams in which two targets were detected were perceived as longer (depicted in Figure 2, right panel). The number of targets presented did not affect subjective duration of the stream, meaning there was no difference in perceived duration between the conditions one target presented / one reported and two targets presented / one reported.

Experiment II showed that duration judgments reflected the actual sequence duration. Furthermore, the results confirmed the temporal dilation effect found in Experiment I and showed that the effect mostly occurred at intermediate sequence durations. At intermediate durations, the duration of the test sequence is most similar to the duration of the standard, which makes the duration judgment task most difficult. The results of Experiment II rule out a duration-independent response bias, which supposedly would have caused equal dilation at all sequence durations.

Experiment III showed a classical attentional blink effect: a second target was detected less often than a first target (of different identity). The results show that even when the task was to report the identity of the targets and not their number, the number of identified targets affected the subjective duration of the sequence. This shows that the temporal dilation effect found in the preceding experiments is not confounded by the numerical response in the target counting task. Again, the effect was maximal at intermediate sequence durations.

4.1.4 Discussion

The three experiments summarized here constitute a novel approach to the study of interval timing. For the first time the effects of automatic stimulus processing and conscious perception of these stimuli are assessed in one paradigm. We demonstrated that the perceived duration of a sequence of items was affected by the number of targets *detected* in the stream, but not by the number of targets *presented*. This finding indicates that only stimuli which traversed the full processing stream and reached consciousness dilated subjective duration. The results are in line with the suggestion that the number of *per-*

ceived changes determines the duration of a time interval (Fraisse, 1963). They refine this suggestion, showing that only *consciously perceived* changes contribute to perceived duration.

The finding that the effect of stimulus dynamics on perceived duration is contingent on conscious perception of these dynamics is a first hint that perceived duration of visual stimuli does not emerge from sensory stimulus processing of these stimuli in visual areas. The findings can be explained by an internal clock model that includes an attentional switch (Block and Zakay, 1997; Church, 1984). According to this model attention allocated to the content of a temporal interval enhances the number of pulses flowing from a pacemaker (through the switch) into the accumulator and therefore the interval is judged as longer. Similar results have been reported for odball stimuli, which attract enhanced attention and are perceived as dilated (Tse et al., 2004).

Study I was designed to distinguish between the effects of perceptual stimulus processing probed at different levels on perceived duration of the same stimuli. A critical point that should be raised is that we only assumed that missed targets were still processed at an automatic sensory level, but did not explicitly test this assumption. Therefore, we conducted a second study, in which we added a measure of the neural processing of visual stimulus dynamics, in order to explicitly assess the magnitude of the neural response to dynamic stimuli and its relation to the perceived duration of the same stimulus.

4.2 Study II: How long depends on how fast - perceived flicker dilates subjective duration

4.2.1 Background

Study II was conducted to separate the effects of the objective rate of stimulus dynamics from the neural processing, as well as from the conscious perception of these dynamics. To examine the relationship between stimulus dynamics and perceived duration we studied the effect of visual flicker on subjective duration. We chose visual flicker, because it has been shown to affect subjective duration (Kanai et al., 2006) and because flickering stimuli allow to quantify objectively the amount of change present in the stimulus as the temporal frequency of the flicker. Furthermore, the sensory visual processing of flicker can be assessed by a well-defined neural correlate, the steady state visual evoked potential (SSVEP) measured in the EEG.

Two thresholds for flicker perception can be assessed: the perceptual flicker fusion threshold (Landis, 1954), and the neural SSVEP threshold. The perceptual flicker fusion threshold is the highest frequency at which an observer consciously perceives the flickering. The SSVEP threshold is the highest frequency that evokes a frequency-specific neural response in the EEG. Importantly, the individual SSVEP threshold is often higher than the individual flicker fusion threshold, which indicates that there is a range of frequencies that are processed as flicker on an early sensory level, but not consciously perceived as flicker (Gur and Snodderly, 1997; Jiang et al., 2007). We were especially interested in whether flicker in this range of frequencies affects perceived duration.

We assessed perceived duration of flickering stimuli at a broad range of frequencies below, in between, and above the flicker-fusion and SSVEP thresholds. This allowed us to test three conflicting assumptions concerning the relationship between the processing of visual stimulus dynamics and perceived duration (see Figure 3): (1) Perceived duration is related to the objective frequency. This assumption would be supported by a monotonous linear increase of perceived duration with flicker frequency. This account does not specify whether the effect lasts until the flicker fusion threshold or the SSVEP threshold (visualized in Figure 3, left panel). (2) Perceived duration is related to the subjective saliency of the flicker (i.e. its subjective strength), which would predict the strongest dilation effect at lower frequencies (visualized in Figure 3, middle panel). (3) Perceived duration is related to the sensory processing of the flicker, which would predict that even flicker frequencies that are not consciously perceived as flicker dilate subjective duration as long as they evoke a neural response (visualized in Figure 3, right panel). Furthermore, sensory models of interval timing predict that the neural energy evoked by the encoding of the stimulus is related to its perceived duration. We therefore tested whether the amplitude of the SSVEP is related to perceived duration.

4.2.2 Methods

We presented flickering visual stimuli to assess the influence of sensory visual processing on duration perception. Flicker was presented with custom-built flicker goggles, which allowed to stimulate the whole visual field on both eyes in parallel, and at a broad range of frequencies. Three measures of interest were acquired in three experimental phases.

First, we assessed the SSVEP threshold as the highest frequency at which we can measure a frequency-specific EEG response. Therefore, we presented 30 s of flickering

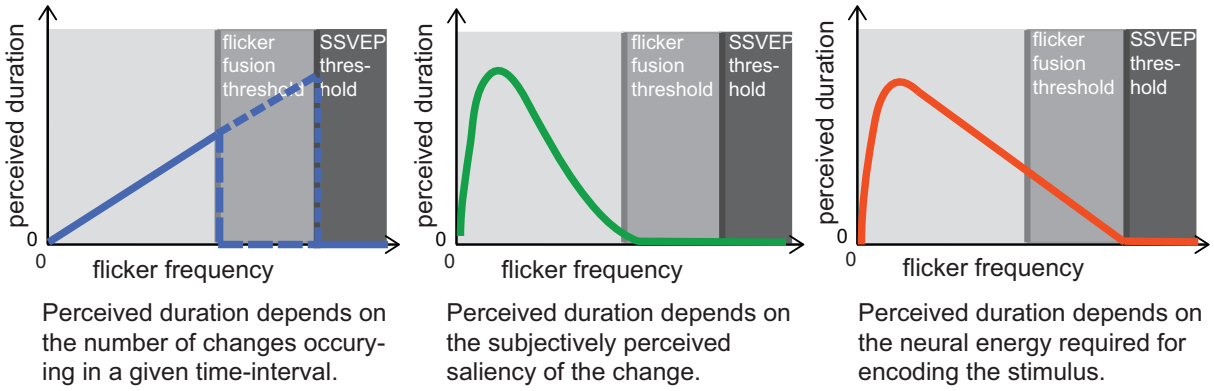

Figure 3: **Study II: Three accounts describing the hypothetical effect of flicker frequency on perceived duration** (adapted from Herbst et al. (2013)). We hypothesized that the effect of flicker on perceived duration could be determined by (1) the objective frequency of the flicker (left panel), leading to a monotonous increase of perceived duration with flicker. This account does not specify whether the effect lasts until the flicker fusion threshold or the SSVEP threshold. (2) The effect of flicker on perceived duration could be determined by the subjective saliency of the flicker (i.e. the subjective strength of the flicker, see middle panel). This would lead to a larger dilation effect at slow frequencies. (3) The effect of flicker on perceived duration is determined by the neural response to the flicker (right panel). This would lead to an effect of flicker on perceived duration, even beyond the flicker fusion threshold.

light at frequencies ranging from 8 to 166 Hz. SSVEP were measured as the amplitude of the power spectrum at the stimulation frequency. Using a bootstrap procedure, we tested whether a given frequency evoked a significant SSVEP.

Second, we assessed the behavioural flicker fusion threshold. We presented 2 s of flickering light at the same frequency range as above and asked participants to rate each stimulus as flickering versus steady. We fitted psychometric functions to the proportion of responding "flicker" and quantified the flicker fusion threshold as the frequency which was perceived as steady in at least 90% of all trials.

Third, we measured the perceived duration of the flickering stimuli at each frequency. On each trial we presented a 2 s standard stimulus (166 Hz, which was perceived as steady) and a test stimulus of varying duration and frequency (the order of standard and test stimuli was randomized). We used an adaptive staircase procedure to adjust the duration of the test stimulus on each trial and converted the resulting parameter estimates to an absolute measure of perceived duration. Finally, we tested at which frequencies flicker affected perceived duration with respect to the flicker fusion threshold and the SSVEP threshold.

threshold.

4.2.3 Results

Visible flicker strongly dilated perceived duration (by about 30% at 4 Hz). The dilation effect decreased linearly with increasing flicker frequency and disappeared around the flicker fusion threshold (at about 50 Hz). After this threshold, there was no effect of flicker on perceived duration even though we measured a significant SSVEP amplitude at higher frequencies (up to 87 Hz on average). The results support an effect of perceived flicker strength (not objective frequency) on perceived duration (see Figure 4). Correlation analyses showed that perceived duration was related to the individually perceived saliency of the flicker: a participant who was more likely to perceive a given frequency as flicker, was also more prone to judge the stimuli of this frequency as longer. For the SSVEP amplitude, we did not find a similar relation: participants who showed a larger SSVEP amplitude in response to a given frequency did not perceive the stimuli of this frequency as longer (nor as shorter; there was no correlation).

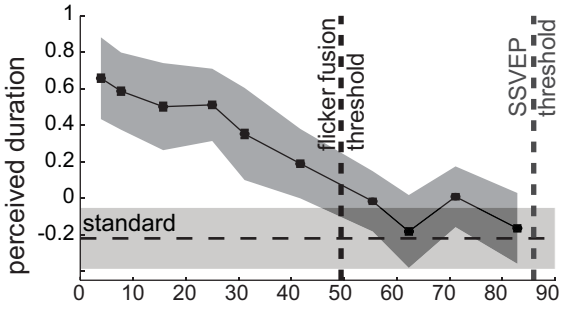

Figure 4: **Study II: Results** (adapted from Herbst et al. (2013)). Perceived duration at each frequency. Flicker dilated perceived duration (indicated on the y-axis) most strongly at the slowest frequencies (indicated on the x-axis). The effect decreased linearly with increasing flicker frequency and was present only until the flicker fusion threshold. In accordance with the subjective saliency account (2, see Figure 3), the subjective strength of the flicker determines the effect of flicker on perceived duration. The gray shade depicts the 95% confidence interval of the estimate of perceived duration. The vertical dashed lines indicate the average flicker fusion threshold and the average SSVEP threshold. The horizontal dashed line indicates the perceived duration of a standard stimulus which was always perceived as steady.

4.2.4 Discussion

The results of Study II show that perceived duration is related to the conscious perception of flicker, but not to its objective frequency, or the neural response evoked by the flicker. Our findings show that stimulus dynamics significantly affected perceived duration, but this effect was contingent on the subjectively perceived strength of the flicker and not on the objective amount of changes presented. A relationship between neural processing of the flicker and perceived duration, as suggested by sensory timing models, was not found. These findings argue against the assumptions derived from sensory models of interval timing. They are, however, consistent with an internal clock model. The finding that the dilation effect was largest for frequencies which were subjectively perceived as strongest supports the assumption that flicker enhances attention, which affect various modules of an internal clock. It has been suggested that flickering stimuli enhance the speed of the pacemaker of the internal clock, which then emits more pulses during a given time interval (Matthews, 2013). Second, it is conceivable that attention acts on a switch between the pacemaker and the accumulator of the clock (Zakay, 2000), which results in the transmission of more pulses from the pacemaker to the accumulator. Third, it is also possible that flicker does not at all affect the stage of temporal encoding, but rather affects duration perception at the memory or decision level. These stages of temporal processing cannot be distinguished based on the results of the present study. It therefore remains unclear at which processing stage the flicker affected the mechanisms of interval timing. In Study III, we tested whether the flicker dilates subjective duration during temporal encoding or at a later stage.

4.3 Study III: Flicker-induced time dilation does not modulate electrophysiological correlates of temporal encoding

4.3.1 Background

Study III tests assumptions derived from dedicated models of interval timing, which postulate three stages of temporal processing. The first stage represents the process of temporal encoding, during which temporal pulses emitted by a pacemaker are counted by an accumulator (also termed the clock stage). Temporal encoding unfolds throughout the time interval, or at least until a criterion duration has elapsed, followed by a memory stage, at which the accumulated pulses are transferred to a working memory store. At a third

stage, the accumulated pulses are compared to a previously memorized reference duration.

Based on the results of the preceding study, we asked if flicker affects duration perception during temporal encoding or whether flicker rather affects the memory or comparison stage after the end of the interval. By assessing just the behavioural response of the participant, these two alternatives cannot be distinguished. Rather, one needs to measure the ongoing process of temporal encoding during stimulus presentation. If flicker dilates duration perception during temporal encoding, it should also affect the neural correlates of temporal encoding. If flicker, however, affects perceived duration at the memory or decision level, the neural correlates of temporal encoding should not be affected by the flicker.

4.3.2 Methods

Flickering stimuli were presented (with the same method as described above), to induce a temporal dilation effect. In this study, we presented stimuli at 4 and 31 Hz, frequencies which had shown to affect perceived duration in the previous study, and at 250 Hz which is known to be perceived as steady. The stimuli were presented in a duration bisection task (Grondin, 2008), in which participants were first familiarized with two reference durations (0.5 and 3.5 s). During the experiment, their task was to categorize stimuli of intermediate durations (from 0.5 to 3.5 s) as either short or long.

We tested whether flicker affected the duration judgments obtained in the bisection task by fitting psychometric functions to the data from the three flicker conditions modelling the proportion of "long" responses as a function of stimulus duration. We compared the point of subjective equality (PSE) across the three flicker conditions. The PSE indicates the criterion duration, at which participants can decide that the stimulus is not short, and therefore must be long. We also compared different models based on the psychometric function to test whether the flicker affects only the threshold of the curve or also the asymptotes. An effect on the threshold would indicate that flicker dilates perceived duration, equivalent to a physical increase in the stimulus' duration.

The event-related EEG data was analysed with a hierarchical linear regression approach (Pernet et al., 2011). This approach allows to analyse single trial data (and not reduce variance by averaging) and to include potentially confounding factors in the regression model. We specified flicker (three levels) and subjective duration (the response given by the participant, two levels) as factors of interest and included stimulus duration

as an additional factor (seven levels). This approach allowed to use the data from all trials in the same model and estimate potential effects at each time point and electrode. To isolate neural correlates of temporal encoding, we contrasted the data from trials judged as long versus short. In a subsequent step, we tested for a an effect of flickering versus steady stimuli. If flicker affects temporal encoding, flicker should also affect the neural correlates of temporal encoding.

4.3.3 Results

Both, the 4 and the 31 Hz flicker significantly affected duration judgments, shown by a leftward shift of the PSE (see Figure 5, left panel). The modelling of the behavioural data shows that flicker affected mostly the threshold of the curve, but not the asymptotes. This indicates that flicker dilated perceived duration equivalent to an actual increase in physical stimulus duration.

The EEG data showed a clear correlate of temporal encoding: an enhanced negativity with a fronto-central topography, whose amplitude was larger for stimuli judged as "long" compared to stimuli judged as "short" (depicted in Figure 2, right panel). This effect occurred prior to the PSE, indicating that it occurred before participants formed a duration judgment. We interpret this effect as a modulation of the amplitude of a contingent negative variation (CNV, Walter et al., 1964) evoked by the timing task. Surprisingly, flicker did not affect the CNV amplitude, which indicates that flicker might not affect temporal encoding. We tested an additional model in which we removed the factor response to assess whether a potential effect of flicker was nested in the response effect. Still, no effect of flicker on the CNV could be found. In sum, the results show that flicker strongly dilates perceived duration, but suggest that this effect does not occur during temporal encoding.

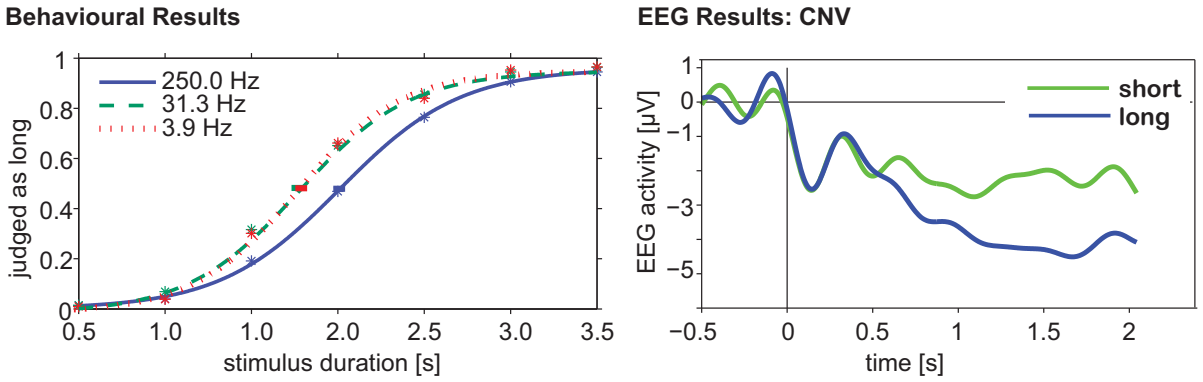

Figure 5: **Study III: Behavioural and EEG results** (adapted from Herbst et al. (2014) with permission from Springer-Verlag GmbH). **Left panel: Behavioural results:** Psychometric functions modelling the proportion of "long" responses as a function of the actual sequence duration. The blue (solid) curve depicts the data from the 250 Hz stimuli, which were perceived as steady. The green (dashed) and red (dotted) curves depict the data from the 31 Hz and 4 Hz conditions, respectively, in which the stimuli were perceived as flicker. Flicker led to a leftward shift of the psychometric function, indicating that it dilated perceived duration. The horizontal lines at the midpoint of each of the functions indicate the 95% confidence intervals. **Right panel:** Illustration of the event related response evoked by the stimuli in this task. Perceived duration affected the amplitude of the CNV component, which is a prolonged negative deflection. Trials judged as "long" (blue line) showed a larger CNV amplitude than trials judged as "short" (green line). Note that in the actual research article, we analysed the data with a general liner model approach, but, for reasons of simplicity, here we show the unmodelled response. Only the data from the 2 s duration are displayed; data were low-pass filtered (at 3 Hz) for better visibility.

4.3.4 Discussion

In this study, we assessed the neural correlates of temporal encoding based on the framework of an internal clock. We tested whether stimulus dynamics affect the process of temporal encoding. Flicker strongly dilated perceived duration, but despite a very robust analysis, we did not find an effect of flicker on the neural correlates of temporal encoding.

We isolated the CNV component as a neural correlate of temporal encoding. In earlier studies the CNV has been described as a neural correlate of temporal encoding and has been specifically linked to the accumulator described in internal clock models (Macar et al., 1999). By showing that the CNV amplitude reflects perceived duration, our results contribute to the ongoing discussion whether the CNV amplitude can be understood as a neural correlate of time perception (Kononowicz and van Rijn, 2011; van Rijn et al., 2011). Our findings argue for a distinction between internal variation of perceived duration and experimentally induced variations of perceived duration. The CNV amplitude seems to reflect only the first type of variation, while effects of stimulus dynamics might affect temporal processing at later stages.

There are a number of possible reasons that may explain why we did not find an effect of flicker on the CNV amplitude. Some of them concern technical issues, such as the fact that flicker induced a strong response in the EEG data, which might have interfered with the comparison of the data between the flicker conditions. However, it is also conceivable that flicker does not affect temporal processing during encoding but affects perceived duration at a later stage. These later stages of temporal processing are less explored than the process of temporal encoding (Wearden, 2004). It has been shown that contextual variables can selectively act at the stage at which the accumulated duration is stored in memory and compared to a previously memorized reference duration (Meck, 1983; Cai and Wang, 2014). Therefore, we tentatively assume that flicker affected perceived duration at the later stage of the process. However, more research is needed to show that stimulus dynamics, such as flicker, really affect the memory stage of temporal processing, and to identify the neural correlates of this stage.

5 General discussion

5.1 Summary of results

Three independent studies were conducted to assess how the visual content of a time interval along with the sensory and cognitive processing triggered by this content influence the perceived duration of the time interval.

Study I confirms previous reports of temporal dilation induced by dynamic stimuli. Importantly, we found that only stimuli that were consciously perceived dilated duration perception, while the stimuli that were (presumably) only processed at the sensory level did not. These findings support the assumption that perceived duration is a function of the number of *consciously perceived* changes during the time interval. The results suggest that temporal dilation was induced by the attentional selection of the stimuli.

Study II tested assumptions derived from sensory models of interval timing by measuring neural correlates of sensory stimulus processing. Frequencies that were consciously perceived as flickering led to a dilation of perceived duration. Furthermore, the dilation effect was correlated with the subjective strength of flicker perception. Opposing the key assumption of sensory timing models, neural correlates of early sensory processing of visual flicker were not related to subjective duration. In line with the results of Study I, we interpret these findings as an interaction between stimulus dynamics and subjective duration at cognitive rather than sensory processing levels.

Study III showed that the amplitude of the contingent negative variation (CNV), identified as a neural correlate of temporal encoding, was not modulated by flicker-induced time dilation. The CNV amplitude reflected only internal variation of perceived duration. Since flicker did not affect the CNV amplitude, it is conceivable that flicker does not affect the process of temporal encoding, but rather affects the mechanisms of duration perception at later stages.

The combined results suggest that the relationship between sensory processing of the content of a time interval and perceived duration of this time interval was overestimated. The effect of stimulus dynamics on duration perception depends on conscious perception of these dynamics. In light of the results presented here, it is difficult to maintain the assumption of a direct connection between early sensory stimulus processing and subjective duration. Therefore, we seem to have a sense of time that functions independently of sensory processing, rather than a sense of change that is directly coupled to the sensory

content perceived during a time interval. To integrate our findings, the mechanisms of interval timing must incorporate an interaction between stimulus dynamics and subjective duration at a higher processing level, which at the moment is only achieved explicitly by so-called dedicated models of interval timing.

Our results are in line with the assumption of a centralized timing mechanism that is not directly coupled to perceptual processing in sensory areas, but can be affected by perceptual processing of visual stimuli at cognitive levels. In particular, the results of Study III can be better explained in the framework of dedicated timing models, which assume two stages of temporal processing, rather than by distributed timing models, which do not explicitly assume two stages. Although numerous alternative models have been proposed, the idea of the internal clock is still present and has not been replaced by a dominant alternative model. As John Wearden, a major advocate of the internal clock model, puts it: *"one might say that if people don't have a pacemaker-accumulator internal clock, they certainly behave as if they do, so any model which replaces this clock idea will have to account for the data which seems to support pacemaker-accumulator clocks so compellingly"* (Wearden, 2003).

In the following section, selected findings will be discussed and integrated, going beyond the discussion of each individual study in the previous section. I will discuss the role of attention in temporal processing, which — as suggested by the findings of Study I — might be more important than one might assume based on the limited discussion of this factor in the timing literature. I will discuss why our findings from Studies I and II do not support sensory models of interval timing, and how the assumptions of these models could be refined. The fourth and fifth discussion points are dedicated to the specific processes postulated by internal clock models which were addressed in Study III: temporal accumulation and temporal memory and decision making processes. Finally, I will raise some limitations of the Studies presented and the approach to the study of timing in general, and provide suggestions on how to improve the research on timing.

5.2 Effects of attentional processing on duration perception

The results of Study I suggest that attention allocated to the stimuli in a sequence resulted in temporal dilation of the whole sequence. Effects of attention have received surprisingly little consideration in the study of interval timing. Effects of attention on perceived duration have been discussed in the resource-sharing framework, under the assumption that

temporal tasks compete for resources with other ongoing tasks (Buhusi and Meck, 2009). According to these so-called resource-sharing models, a concurrent task should shorten perceived duration, because it leaves fewer resources for the timing task. Sequences in which additional items attracted attention should therefore be perceived as shorter as compared to sequences in which fewer items attracted attention. As opposed to this, we found dilation of perceived duration for sequences which received enhanced attention. Therefore, our findings show that the target detection task and the concurrent duration judgment task do not compete for resources, but rather share the same resource. It seems plausible that attention allocated to the stimulus conveys information that is then used by the mechanisms of interval timing to form an inference on the elapsed duration.

Concerning the results of Studies II and III, it is possible that attention mediates the effect of flicker on perceived duration. It is likely that flickering stimuli attract attention more than static stimuli and that attention is responsible for the dilation effect. Although the exact relationship between flickering stimuli and attention remains unknown, flickering stimuli are often used and interpreted as warning signals (Berg et al., 2007), indicating that they attract attention more than static stimuli. Evidence that stimulus-directed attention affects perceived duration comes from the combined interpretation of two studies: Wittmann et al. (2010) found temporal dilation only for looming but not for receding stimuli. Franconeri and Simons (2003) report that moving and looming stimuli attract attention, while receding objects do not. This double dissociation supports the hypothesis that attention allocated to the content of a time interval is closely related the interval's perceived duration.

The psychophysical analyses of Studies I and III show that the effects of attentional selection and conscious flicker perception on perceived duration resemble the effect of sustained attention on stimulus contrast (Carrasco et al., 2004; Ling and Carrasco, 2006). In contrast detection studies, this effect is described as a "contrast gain" and is interpreted as equivalent to an enhancement of the physical stimulus contrast due to attention. In the domain of timing, this effect is equivalent to a "duration gain", equivalent to an enhancement of the physical stimulus duration through attention.

In light of pacemaker-accumulator models attentional effects on perceived duration could be explained as an acceleration of the clock rate through attention (Tse et al., 2004), or by an attentional switch that enhances the flow of pulses from the pacemaker to the accumulator (Block and Zakay, 1997). The problem is that the two alternatives

cannot be easily distinguished here, since both would result in a greater number of pulses accumulated. The results of Study III suggest that neither of the two options applies and that the dilation effect occurs not during temporal encoding but at later stages of temporal processing (see discussion below).

In the framework of distributed timing models, areas whose activity is enhanced by attention could provide information about their duration. Obviously, the problem with this assumption is that it is difficult to quantify and measure attention. Future studies could target the activity in the fronto-parietal attention network (Corbetta, 1998; Ptak, 2012) and test for a relation between the magnitude of activity in this network and perceived duration.

5.3 Evidence contradicting sensory timing models

In part, this work was conducted to test specific assumptions derived from sensory models of interval timing (Bueti, 2011). These models hold that perceived duration is encoded in the neural activity expended in perceptual processing of the content of a time interval (Bueti, 2011; Eagleman and Pariyadath, 2009). Under this assumption, every aspect of the stimulus that triggers a neural response should also affect the stimulus' perceived duration (Bruno et al., 2010; Johnston et al., 2006).

This prediction is contradicted by the finding of Study II, where visual flicker that evokes a frequency-specific neural response but no conscious perception did not affect perceived duration. The highest visual area that is believed to be able to process flicker above the flicker fusion threshold is V4 (Jiang et al., 2007). Since viewing flicker above the flicker fusion threshold did not affect perceived duration, it seems unlikely that duration perception emerges from the activity of any of these low level visual areas. On the contrary, the results of Studies I and II argue for an interaction between visual processing and perceived duration at cognitive levels of perceptual processing.

It is conceivable that perceived duration is encoded in cortical areas higher up the visual processing stream, for example in the frontal eye fields. In a recent report Mayo and Sommer (2013) show that the response strength of individual neurons (and neuronal populations) in monkeys' frontal eye fields is correlated with temporal duration judgments of short durations (shorter than 0.5 s). Frontal eye field activity has also been related to visual awareness (O'Shea and Walsh, 2004) and visual attention (Armstrong and Moore, 2007), but is still specifically related to the processing of visual stimuli (for reviews see

Paus (1996) and Squire et al. (2012)). The frontal eye fields have been described as part of the fronto-parietal attention network (Corbetta and Shulman, 2002; Corbetta, 1998; Ptak, 2012), suggesting a relation between attentional processing in this area and duration perception as evoked above. Further research could therefore target the relationship between the activation of the frontal eye fields and the perceived duration of visual stimuli in humans, possibly including a manipulation of attention.

Another assumption derived from sensory models of interval timing and the neural energy approach (Eagleman and Pariyadath, 2009) claims that the magnitude of the neural response to a stimulus codes for the perceived duration of the stimulus. This assumption has been assessed in Study II, but no correlation between the magnitude of individual SSVEP responses evoked by flicker and perceived duration was found, even at frequencies at which flicker was clearly visible. Of course, this does not completely disprove a relationship between sensory processing and perceived duration. The relationship between the magnitude of the visual response and the perceived duration could be mathematically more complex (Ahrens and Sahani, 2011). Furthermore, it could be that the phase, rather than the amplitude of the periodic response triggered by the flickering stimulus contains information relevant for perceived duration. Evidence about the encoding of temporal aspects in the phase of neuronal oscillations comes from recent reports, linking the phase of neural oscillations to temporal expectations (Rohenkohl and Nobre, 2011) and the perception of rhythm (Henry and Herrmann, 2013).

As stated in the Introduction, the neural energy approach does not provide distinct hypotheses about the nature of the neural activity in which durations are encoded. The idea that duration perception is derived from the activity related to sensory processing of the stimulus is only one interpretation of this account. The large number of processes and regions whose neural activity could be relevant for timing makes it almost impossible to conclusively test this approach. It is even conceivable that the activity containing the code for perceived duration is largely distributed across the whole brain and relies on dynamics that are difficult to assess with techniques currently available for neuroimaging.

5.4 Ramping neural activity reflects temporal accumulation

Study III provided insights into the neuro-cognitive mechanisms of temporal encoding, which seem to cumulate in the amplitude of the CNV. Earlier studies have described the CNV component as related to the accumulation of temporal pulses (Macar et al., 1999;

Macar and Vidal, 2002) in pacemaker-accumulator models. Larger CNV amplitudes reflect subjectively elapsed time, with more negative amplitudes reflecting longer perceived duration. However, the CNV amplitude seems to reflect only internal variation in perceived duration, but does not appear to reflect the temporal dilation effect induced by the dynamic stimuli. Recently, a failed attempt to replicate the findings reported by Macar et al. (1999), undertaken by Kononowicz and van Rijn (2011) evoked a discussion about whether the CNV amplitude is a specific correlate of temporal processing, or whether it generally reflects response preparation. Our findings contribute to this discussion by showing that the amplitude of the CNV is specifically related to the internal variation of perceived duration during a time interval.

Slow changes of neural activity, as represented by the CNV, appear to be a biologically and theoretically plausible mechanism for temporal processing. For instance, Reutimann et al. (2004) showed that single neurons can code for durations much longer than the individual firing rate by changes in the magnitude of their response across time. It has also been shown mathematically that patterns of firing within neuronal populations can code for duration (Buonomano and Laje, 2010; Laje et al., 2011). Ramping neuronal activity related to subjective time has been studied experimentally in monkeys (Mita et al., 2009) as well as in humans (Wittmann, 2013). In sum, slowly accumulating activity appears to be a good model for the accumulation of duration over a time interval.

The CNV is typically measured at fronto-central electrodes and has been ascribed to the activation of the supplementary motor area (SMA, Macar et al., 1999), which is one of the key candidates for brain areas involved in timing. A recent comprehensive meta-analysis (based on different imaging techniques) concluded that the SMA was the only region activated across different timing tasks (Wiener et al., 2010). Furthermore, recordings from preSMA and SMA in monkeys, (Mita et al., 2009) have shown that ramping activity in single neurons located in these regions codes for perceived duration.

In sum, the SMA seems to play a key role in temporal processing, reflected by ramping activity measured in this region during timing tasks. The emission of pulses might be distributed amongst many areas, depending on the content of the relevant time interval, the task used to study timing, or other factors like attention allocated to the stimulus. However, the accumulation might take place in motor areas, like the SMA in a centralized rather than distributed way.

5.5 Temporal processing after encoding

The observations of Study III can be best explained by a model that separates the stage of temporal encoding from the stage at which the temporal information is transformed into a temporal decision. Such a distinction is provided by dedicated models of interval timing, which postulate that after temporal encoding, accumulated information is transferred to a representation in working memory. The representation in working memory is then compared to the representation of a reference duration, or a temporal scale. The exploration of these later mechanisms of temporal processing has received less interest in the study of interval timing (Wearden, 2004), but is important for understanding how information accumulated during a time interval can be transferred into a behavioural duration judgment. It is conceivable that at least part of the effects of stimulus dynamics described in the introduction actually affect temporal processing at later stages. Research on temporal processing in animals has shown that the memory stage can be selectively affected by specific drugs (Meck, 1983). Recently, Cai and Wang (2014) showed that with human participants, numerical stimulus magnitude selectively biases the stage at which a representation of the stimulus duration is formed in memory, but does not affect the retrieval of this representation. It is thus conceivable that the flicker presented in Studies II and III affects the memory representation of the stimulus and therefore biases the comparison with the memorized reference durations (that were learned based on non-flickering stimuli). This assumption could easily be tested by presenting reference durations at variable frequencies and testing whether the relative difference in frequency between the reference duration and the test duration explains the temporal dilation.

5.6 Limitations and suggestions for further research

Part of the work described here — especially the tests of hypotheses derived from sensory models of interval timing — resulted in so-called negative findings, which are no less important than positive findings. They are, however, harder to interpret and much harder to communicate. The exact mechanisms of interaction between visual perceptual processing and temporal processing might still seem like a black box, but our work has contributed to narrowing the box by excluding the very early sensory stage from the list of likely candidates. It would be interesting to validate the findings presented here with different approaches. For example, it would be preferable to acquire a less explicit mea-

sure of perceived duration. Currently, participants in timing studies are asked to verbalize their duration judgments, or express them in a dichotomous form. Maybe if we had more sensitive assessment techniques for perceived duration more subtle effects, like the one of invisible flicker on perceived duration, could be measured.

The three studies presented here, employ timing tasks and measures to assess the questions of interest from different points of view. It is difficult to interpret and integrate the results acquired with different tasks and measurements. However, this diversity reflects very well the literature on temporal processing, embracing many different tasks and different analysis techniques, making assumptions about different models, and examining different ranges of duration. Thus, the literature on temporal processing is extremely scattered and an effort should be made to classify and review the present reports, according to the underlying models, the tasks used, and the time range of interest.

Despite copious effort put in the study of temporal processing, we are far from understanding the mechanisms underlying the ubiquitous percept of time. A recent report states: *"Indeed, given the diversity of the competing models, one may be inclined to state that researchers are actually clueless concerning the question of how the brain processes time"* (Wittmann, 2013). Why is it so difficult to study the mechanisms of temporal processing? One of the problems is that no one really knows what time is. We cannot measure time, as we can measure light or sound waves, but the devices built to measure times (clocks) actually create their own time based on an internal rhythm. There is no such thing as a purely temporal stimulus that could be used in psychological experiments. When asking participants to judge perceived duration, we have to present lights or tones, or other sensory stimuli. As shown by this work and many others, all these aspects of the stimuli have influence on perceived duration and make it difficult to study pure timing in the sense of William James. On the other hand, time is always present, and temporal processing might underlie many (if not most) cognitive functions. Therefore, temporal processing cannot be studied in isolation. An interdisciplinary effort is required to frame the important questions that need to be answered, to develop better models of timing and to study the brain processes associated with it.

Timing has been studied as a perceptual process, although we know that time cannot be perceived like light or sound. The localisation of temporal accumulation in areas that are associated with motor functions might imply that timing is in general more related to motor behaviour than to perception. A recent study which has shown that temporal

estimates are more precise for pictures that imply action than for still pictures (Moscatelli et al., 2011) supports a close relationship between timing and motor behaviour. The passive perception of duration as it is currently assessed by timing tasks is probably not a good model of the timing behaviour that is important for the successful interaction with a dynamic environment. Since time is most important when interacting with the world, we should probably study time more in the way we study motor action. Instead of assessing duration judgments, we should probably focus on temporal expectations, which might provide a more ecologically valid measure to study temporal processing in the brain.

5.7 Conclusions

In hindsight, we can now say that the mechanisms of sensory perception and the mechanisms of duration perception are more distinct than assumed at the outset of this work. Sensory models of interval timing provide the appealing hypothesis, that duration is encoded in the activation triggered by processing of sensory stimuli (whose duration we are timing). However, here we have demonstrated that this is not the case. Perceived changes seem to influence duration perception in a much more abstract way, possibly mediated by attention. Future studies should investigate temporal processing more with respect to the function it subserves in a dynamic environment than as a passive percept, which might require an interdisciplinary effort. This effort should be worthwhile, since solving the puzzle of subjective time will greatly enhance our understanding of the brain.

References

Ahrens, M. and Sahani, M. (2011). Observers exploit stochastic models of sensory change to help judge the passage of time. *Current Biology*, 21(3):200–206.

Allan, L. G. and Kristofferson, A. B. (1974). Psychophysical theories of duration discrimination. *Perception & Psychophysics*, 16(1):26–34.

Armstrong, K. M. and Moore, T. (2007). Rapid enhancement of visual cortical response discriminability by microstimulation of the frontal eye field. *Proceedings of the National Academy of Sciences*, 104(22):9499–9504.

Berg, W. P., Berglund, E. D., Strang, A. J., and Baum, M. J. (2007). Attention-capturing properties of high frequency luminance flicker: Implications for brake light conspicuity. *Transportation Research Part F: Traffic Psychology and Behaviour*, 10(1):22–32.

Block, R. and Zakay, D. (1997). Prospective and retrospective duration judgments: A meta-analytic review. *Psychonomic Bulletin & Review*, 4(2):184–197.

Block, R. A. and Zakay, D. (1996). Models of psychological time revisited. *Time and Mind*, 33:171–195.

Brown, S. (1995). Time, change, and motion: The effects of stimulus movement on temporal perception. *Attention, Perception, & Psychophysics*, 57(1):105–116.

Bruno, A., Ayhan, I., and Johnston, A. (2010). Retinotopic adaptation-based visual duration compression. *Journal of Vision*, 10(10).

Bueti, D. (2011). The sensory representation of time. *Frontiers in Integrative Neuroscience*, 5.

Bueti, D., Bahrami, B., and Walsh, V. (2008). Sensory and association cortex in time perception. *Journal of Cognitive Neuroscience*, 20(6):1054–1062.

Buhusi, C. and Meck, W. (2005). What makes us tick? functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, 6(10):755–765.

Buhusi, C. and Meck, W. (2009). Relative time sharing: new findings and an extension of the resource allocation model of temporal processing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525):1875–1885.

Buonomano, D. and Laje, R. (2010). Population clocks: motor timing with neural dynamics. *Trends in Cognitive Sciences*, 14(12):520–527.

Cai, Z. G. and Wang, R. (2014). Numerical magnitude affects temporal memories but not time encoding. *PloS one*, 9(1):e83159.

Carrasco, M., Ling, S., and Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, 7(3):308–313.

Chun, M. (1997). Types and tokens in visual processing: A double dissociation between the attentional blink and repetition blindness. *Journal of Experimental Psychology: Human Perception and Performance*, 23(3):738.

Church, R. (1984). Properties of the internal clock. *Annals of the New York Academy of Sciences*, 423(1):566–582.

Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences*, 95(3):831–838.

Corbetta, M. and Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3):201–215.

Coull, J., Vidal, F., Nazarian, B., and Macar, F. (2004). Functional anatomy of the attentional modulation of time estimation. *Science*, 303(5663):1506.

Creelman, C. D. (1962). Human discrimination of auditory duration. *The Journal of the Acoustical Society of America*, 34:582.

Eagleman, D. and Pariyadath, V. (2009). Is subjective duration a signature of coding efficiency? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525):1841.

Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinion in Neurobiology*, 18(2):131–136.

Fraisse, P. (1963). *The psychology of time.* Lowe & Brydone (Printers), London.

Franconeri, S. L. and Simons, D. J. (2003). Moving and looming stimuli capture attention. *Perception & Psychophysics*, 65(7):999–1010.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, 84(3):279.

Grill-Spector, K., Henson, R., and Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, 10(1):14–23.

Grondin, S. (1993). Duration discrimination of empty and filled intervals marked by auditory and visual signals. *Perception & Psychophysics*, 54:383–349.

Grondin, S. (2008). Methods for studying psychological time. *Psychology of Time*, pages 51–74.

Grondin, S. (2010). Timing and time perception: A review of recent behavioral and neuroscience findings and theoretical directions. *Attention, Perception, & Psychophysics*, 72(3):561.

Gur, M. and Snodderly, D. M. (1997). A dissociation between brain activity and perception: chromatically opponent cortical neurons signal chromatic flicker that is not perceived. *Vision Research*, 37(4):377–382.

Guyau, J. (1890). *La genèse de l'idée de temps.* Alcan, Paris.

Harrington, D. L., Haaland, K. Y., and Hermanowitz, N. (1998). Temporal processing in the basal ganglia. *Neuropsychology*, 12(1):3.

Henry, M. and Herrmann, B. (2013). Low-frequency neural oscillations support dynamic attending in temporal context. *Timing & Time Perception*.

Herbst, S. K., Chaumon, M., Penney, T. B., and Busch, N. A. (2014). Flicker-induced time dilation does not modulate eeg correlates of temporal encoding. *Brain topography*, pages 1–11.

Herbst, S. K., Javadi, A. H., van der Meer, E., and Busch, N. A. (2013). How long depends on how fast — perceived flicker dilates subjective duration. *PloS one*, 8(10):e76074.

Herbst, S. K., van der Meer, E., Busch, N. A., et al. (2012). Attentional selection dilates perceived duration. *Perception*, 41(8):883.

Hinton, S. C. and Meck, W. H. (1997). The internal clocks of circadian and interval timing. *Endeavour*, 21(2):82–87.

Ivry, R. and Schlerf, J. (2008). Dedicated and intrinsic models of time perception. *Trends in Cognitive Sciences*, 12(7):273–280.

Ivry, R. B. and Hazeltine, R. E. (1995). Perception and production of temporal intervals across a range of durations: evidence for a common timing mechanism. *Journal of Experimental Psychology: Human Perception and Performance*, 21(1):3.

Ivry, R. B., Spencer, R. M., Zelaznik, H. N., and Diedrichsen, J. (2002). The cerebellum and event timing. *Annals of the New York Academy of Sciences*, 978(1):302–317.

James, W. (1891). *The principles of psychology*, volume 1. Harvard University Press.

Jiang, Y., Zhou, K., and He, S. (2007). Human visual cortex responds to invisible chromatic flicker. *Nature Neuroscience*, 10(5):657–662.

Johnston, A., Arnold, D., and Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology*, 16(5):472–479.

Kanai, R., Paffen, C., Hogendoorn, H., and Verstraten, F. (2006). Time dilation in dynamic visual display. *Journal of Vision*, 6(12).

Kaneko, S. and Murakami, I. (2009). Perceived duration of visual motion increases with speed. *Journal of Vision*, 9(7).

Kanwisher, N. G. (1987). Repetition blindness: Type recognition without token individuation. *Cognition*, 27(2):117–143.

Kelly, S. (2005). *Cognition and the Brain: The Philosophy and Cognition and the brain: The philosophy and neuroscience movement.*, chapter 6, pages 208 – 240. Cambridge University Press, New York and Cambridge.

Kononowicz, T. W. and van Rijn, H. (2011). Slow potentials in time estimation: the role of temporal accumulation and habituation. *Frontiers in Integrative Neuroscience*, 5:48.

Laje, R., Cheng, K., and Buonomano, D. (2011). Learning of temporal motor patterns: an analysis of continuous versus reset timing. *Frontiers in Integrative Neuroscience*, 5:61.

Landis, C. (1954). Determinants of the critical flicker-fusion threshold. *Physiological Reviews*, 34(2):259–286.

Lewis, P. and Miall, R. (2006). A right hemispheric prefrontal system for cognitive time measurement. *Behavioural Processes*, 71(2):226–234.

Ling, S. and Carrasco, M. (2006). Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision research*, 46(8-9):1210–1220.

Macar, F. and Vidal, F. (2002). Time processing reflected by EEG surface laplacians. *Experimental Brain Research*, 145(3):403–406.

Macar, F. and Vidal, F. (2004). Event-related potentials as indices of time processing: a review. *Journal of Psychophysiology*, 18(2):89–104.

Macar, F., Vidal, F., and Casini, L. (1999). The supplementary motor area in motor and sensory timing: evidence from slow brain potential changes. *Experimental Brain Research*, 125(3):271–280.

Matthews, W. (2011). How do changes in speed affect the perception of duration? *Journal of Experimental Psychology: Human Perception and Performance*, 37(5):1617.

Matthews, W. J. (2013). How does sequence structure affect the judgment of time? exploring a weighted sum of segments model. *Cognitive Psychology*, 66(3):259–282.

Mauk, M. and Buonomano, D. (2004). The neural basis of temporal processing. *Annual Reviews in Neuroscience*, 27:307–340.

Mayo, J. P. and Sommer, M. A. (2013). Neuronal correlates of visual time perception at brief timescales. *Proceedings of the National Academy of Sciences*, 110(4):1506–1511.

McAdam, D. (1966). Slow potential changes recorded from human brain during learning of a temporal interval. *Psychonomic Science*, 6.9:435–436.

Meck, W. H. (1983). Selective adjustment of the speed of internal clock and memory processes. *Journal of Experimental Psychology: Animal Behavior Processes*, 9(2):171.

Michon, J., Pouthas, V., and Jackson, J. (1988). *Guyau and the idea of time.* North-Holland.

Mita, A., Mushiake, H., Shima, K., Matsuzaka, Y., and Tanji, J. (2009). Interval time coding by neurons in the presupplementary and supplementary motor areas. *Nature Neuroscience*, 12(4):502–507.

Moscatelli, A., Polito, L., and Lacquaniti, F. (2011). Time perception of action photographs is more precise than that of still photographs. *Experimental Brain Research*, 210(1):25–32.

Münsterberg, H. (1889). *Beiträge zur experimentellen Psychologie*, volume 1. JCB Mohr.

Ng, K. K., Tobin, S., and Penney, T. B. (2011). Temporal accumulation and decision processes in the duration bisection task revealed by contingent negative variation. *Frontiers in integrative neuroscience*, 5:77.

O'Shea, J. and Walsh, V. (2004). Visual awareness: the eye fields have it? *Current Biology*, 14(7):R279–R281.

Pariyadath, V. and Eagleman, D. (2007). The effect of predictability on subjective duration. *PLoS One*, 2(11):e1264.

Paus, T. (1996). Location and function of the human frontal eye-field: a selective review. *Neuropsychologia*, 34(6):475–483.

Penton-Voak, I., Edwards, H., Percival, A., and Wearden, J. (1996). Speeding up an internal clock in humans? effects of click trains on subjective duration. *Journal of Experimental Psychology: Animal Behavior Processes*, 22(3):307.

Pernet, C. R., Chauveau, N., Gaspar, C., and Rousselet, G. A. (2011). LIMO EEG: a toolbox for hierarchical LInear MOdeling of ElectroEncephaloGraphic data. *Computational Intelligence and Neuroscience*, 2011:3.

Pöppel, E. (1978). Time perception. In *Perception*, pages 713–729. Springer.

Prins, N. et al. (2009). *Psychophysics: a practical introduction*. Academic Press.

Ptak, R. (2012). The frontoparietal attention network of the human brain action, saliency, and a priority map of the environment. *The Neuroscientist*, 18(5):502–515.

Rammsayer, T. H. and Lima, S. D. (1991). Duration discrimination of filled and empty auditory intervals: Cognitive and perceptual factors. *Perception & Psychophysics*, 50(6):565–574.

Raymond, J., Shapiro, K., and Arnell, K. (1992). Temporary suppression of visual processing in an RSVP task: an attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, 18(3):849.

Reutimann, J., Yakovlev, V., Fusi, S., and Senn, W. (2004). Climbing neuronal activity as an event-based cortical representation of time. *The Journal of neuroscience*, 24(13):3295–3303.

Roeckelein, J. (2000). *The concept of time in psychology: A resource book and annotated bibliography*. Greenwood Pub Group.

Rohenkohl, G. and Nobre, A. C. (2011). Alpha oscillations related to anticipatory attention follow temporal expectations. *The Journal of Neuroscience*, 31(40):14076–14084.

Shapiro, K., Driver, J., Ward, R., and Sorensen, R. E. (1997). Priming from the attentional blink: A failure to extract visual tokens but not visual types. *Psychological Science*, 8(2):95–100.

Squire, R. F., Steinmetz, N. A., and Moore, T. (2012). Frontal eye field. *Scholarpedia*, 7(10):5341.

Staddon, J. and Higa, J. (1999). Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior*, 71(2):215–251.

Treisman, A. and Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1):97–136.

Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the "internal clock". *Psychological Monographs: General & Applied*, 77(13):1–31.

Tse, P., Intriligator, J., Rivest, J., and Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception & Psychophysics*, 66(7):1171–1189.

van Rijn, H., Kononowicz, T. W., Meck, W. H., Ng, K. K., and Penney, T. B. (2011). Contingent negative variation and its relation to time estimation: a theoretical evaluation. *Frontiers in Integrative Neuroscience*, 5:91.

Walter, W., Cooper, R., Aldridge, V., McCallum, W., and Winter, A. (1964). Contingent negative variation: an electric sign of sensori-motor association and expectancy in the human brain. *Nature*, 203:380–384.

Wearden, J. (2003). *Applying the scalar timing model to human time psychology: Progress and challenges*. Hogrefe & Huber Publishers.

Wearden, J. H. (2004). Decision processes in models of timing. *Acta Neurobiologiae Experimentalis*, 64(3):303–318.

Wichmann, F. and Hill, N. (2001a). The psychometric function: I. fitting, sampling, and goodness of fit. *Perception & Psychophysics*, 63(8):1293–1313.

Wichmann, F. and Hill, N. (2001b). The psychometric function: Ii. bootstrap-based confidence intervals and sampling. *Perception & Psychophysics*, 63(8):1314.

Wiener, M., Turkeltaub, P., and Coslett, H. B. (2010). The image of time: a voxel-wise meta-analysis. *Neuroimage*, 49(2):1728–1740.

Wittmann, M. (2013). The inner sense of time: how the brain creates a representation of duration. *Nature Reviews Neuroscience*, 14(3):217–223.

Wittmann, M., Virginie van Wassenhove, A., and Paulus, M. (2010). The neural substrates of subjective time dilation. *Frontiers in Human Neuroscience*, 4.

Xuan, B., Zhang, D., He, S., and Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision*, 7(10).

Zakay, D. (2000). Gating or switching? gating is a better model of prospective timing (a response to "switching or gating?" by Lejeune). *Behavioural Processes*, 50(1):1–7.

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig und ohne unerlaubte Hilfe verfasst habe;

dass ich die Doktorarbeit an keiner anderen Universität eingereicht habe und keinen Doktorgrad in dem Promotionsfach Psychologie besitze;

und dass mir die zugrunde liegende Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät II vom 17.01.2005, zuletzt geändert am 13.02.2006, veröffentlicht im Amtlichen Mitteilungsblatt der HU Nr. 34/2006, bekannt ist.

Sophie Herbst
Berlin, den 27.März 2014